

ANATOMY OF XYLEM AND PHLOEM OF THE DATISCACEAE¹

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ABSTRACT: The woods of *Octomeles* and *Tetrameles* are similar in appearance and gross morphology. The large diameters and thin walls of the vessel elements and libriform fibers are responsible for the light-weight, non-durable quality of the woods; the small amount of wood parenchyma present probably does not contribute appreciably to this condition. The woods are quantitatively different in several respects, for instance in fiber length and vessel element diameter. The cambium is more conspicuously storied in *Tetrameles* than in *Octomeles*. The wood of *Datisca* is different from that of the two monotypic tree genera in the family and is similar to that of some other "woody herbs." The secondary phloem regions of *Octomeles* and *Tetrameles* are strikingly similar in the zone of functional sieve tube elements, but the amount and distribution of sclerenchyma in the zone of sieve tube obliteration are different.

INTRODUCTION

Lindley in 1846 suggested a relationship between *Datisca* and *Begonia* based on his knowledge of little more than the obvious morphological features, and even a detailed study of floral and vegetative parts by the present writer (Davidson 1973) permitted only an educated guess about the systematic position of the Datisceae and the closeness of interfamilial ties. Many of the same trends and features are present in Datisceae and Begoniaceae and in Flacourtiaceae, e.g., tendency toward an inferior ovary, monoecy and dioecy, separate stigmas, capsular fruits, numerous anatropous ovules and seeds, inflorescences with many flowers, tendency toward anemophily, valvate sepals, and nectar glands between gynoecium and androecium; but it is the plasticity of just such traditionally reliable characteristics in conjunction with the small size of the two families Datisceae and Begoniaceae that has made placement difficult, and not simply a lack of basic information.

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The four species of the Datisceae are trees or root perennials. *Datisca cannabina* L., a root perennial, has a range extending from the Middle East through Iran and Afghanistan and into Nepal. This species was not available for study, and therefore the California species, *D. glomerata* (Presl) Baill., which sometimes develops a small amount of wood, was used. *Octomeles sumatrana* Miq. and *Tetrameles nudiflora* R. Br. are monotypic genera of Indo-Malesian trees attaining heights of 150 to 180 feet. The former grows in rain forest and the latter in monsoon forest. Both trees are dioecious, a phenomenon explained (Davidson 1973) as a response to selection for maximum outbreeding in essentially insular situations; and this explanation could also account for dioecy in *D. cannabina* and androdioecy in *D. glomerata*.

In the present study, wood and phloem anatomy are compared among the three genera. Ontogeny of the xylem is analyzed, and comparison is made of the morphological variation in tracheary elements, fibers, and rays from primary to secondary xylem in each genus to see if a basic pattern is present despite the difference in habit between *Datisca* and the two trees. This search has not been entirely unrewarding, but interpretations based on this sort of data must be made with reservation because of the lack of comparable information from larger families that might be used to establish trends or at least the range of variation in a single group. Data derived from measurements of wood elements of *Octomeles* and *Tetrameles* are presented graphically to show size changes from the centers of the trees outward toward the cambia.

MATERIALS AND METHODS

Samples of *Datisca glomerata* were collected in Southern California (Davidson 1002). Wood samples of *Octomeles* and *Tetrameles* were collected during a field trip to Malasia in 1970. Collection data for *Octomeles* is as follows: Davidson 1124, sapling, Gum Gum Forest Reserve, Sabah; Davidson 1126, seedling from Lungmanis grown in shade, Sabah; Davidson 1482, tree from Oomsis Cr., near Port Moresby, New Guinea. Data for *Tetrameles*: Davidson 1413a, tree from Pahang, W. Malaysia; Davidson 1493, tree from Brown River, Papua. Wood samples were taken across the diameter of the bole at a level just above the buttresses, at mid-point 30 to 60 ft above the ground, and at a level below the first branching. Samples from buttresses, limbs, and twigs were also included. Woods were kiln-dried and shipped to the U.S. with paraformaldehyde flake as a preservative. Cambia, phloem tissues, and twigs were preserved in alcohol.

All material was prepared by standard microtechnical procedures. Woods of the two trees sectioned poorly on the sliding microtome and had to be embedded in Parowax. Phloem was stained with safranin-fast green and with lacmoid, following the procedure of Cheadle et al. (1953). Fiber measurements were taken from macerations, but vessel elements were too large to macerate well and had to be studied in tangential sections. All figures represent the average of 50 measurements, except where stated otherwise.

OBSERVATIONS

Octomeles sumatrana Miq.

Xylem.—Fusiform cambial initials from the base of the New Guinea tree used in this study are storied, although the rows are not always perfectly even (Fig. 12). Cambial initials from the seedling and the four-meter sapling are not storied. Ray initials are storied, as are the vessel elements, though in the latter case this is inconspicuous because the vessels are solitary or paired; however, growth and adjustments related to it obscure storying in the rest of the wood elements. Average fusiform initial length and tangential width are $470\ \mu$ and $24\ \mu$, respectively. Corresponding values for ray initials are $780\ \mu$ and $110\ \mu$. In the shade-grown seedling (*Davidson 1126*) the average size of fusiform initials is $250\ \mu$ long and $8\ \mu$ wide.

The following observations on primary xylem are based on serial radial sections and macerations of the xylem of seedling and sapling stems of *Octomeles*. Secondary xylem consisting mostly of libriform fibers arises from the cambium only a few centimeters proximal to the apex, apparently before stem elongation is completed; therefore, it is difficult to distinguish between early secondary elements and the late metaxylem. For convenience an arbitrary topographic boundary is used here. The first elements to arise from the interfascicular parts of the cambium are very long libriform fibers, and therefore, all elements included within the fiber zone opposite the original bundles are considered secondary. An ontogenetic study in depth has not been attempted, and the terms "proto-" and "metaxylem" are avoided. Instead, reference is made to the topographic relationships of the elements discussed as seen in radial sections and in incompletely macerated groups.

Tracheary elements of the primary xylem have annular and helical thickenings. The type of thickening may vary within a single element; and single, double, multiple, and singly-double helices are present in the peripheral part of the bundles (using the terminology of Bierhorst 1960). Perforation plates of the helically thickened elements may be simple (Fig. 1), or they may have a few thin bars.

Elements occurring in radial series adjust to the helically thickened vessel members have scalariform pitting with broad or narrow bars on all faces (Fig. 3). The helical thickenings of the preceding vessels are usually very closely spaced, and the gyres are nearly transverse (Fig. 2). Adjacent to the scalariformly pitted vessel elements are elements with alternate, closely spaced intervascular pits with wide borders and elliptical to narrow inner apertures; or there may be a series of transitional forms with more widely spaced bordered pits and larger apertures. Vessel-parenchyma pitting varies in this transitional region from scalariform with wide, horizontal bars to scalariform with thin, diagonal or variously oriented connections between the larger bars. These elements may be part of the late metaxylem or early secondary xylem. In vessel elements with closely spaced, alternate intervascular pits, the pits opposite parenchyma cells are unilaterally compound and half-bordered, and they are similar in most ways to the vessel-parenchyma pitting in the mature xylem at a greater distance from the pith. The chief difference is that the ray parenchyma near the pith consists mostly of upright cells, and the pits on

the vessels are thus arranged in vertical rows. The perforation plates of the scalariformly pitted elements are almost always transverse, or nearly so, as are those of the first alternately pitted elements adjacent to them; and the ends of the elements are frequently tailed. The maturation pattern described here for the seedling is similar to that found in the xylem taken about two meters above the ground level in the sapling (*Davidson 1124*).

The transition from the scalariformly pitted vessel elements to the first long, alternately pitted vessel elements and to the subsequent shorter, alternately pitted elements takes place within one millimeter of the pith in the sapling. Only a few measurements were possible, but they indicate that the helical elements are the longest ($660\ \mu$; 20 measurements) and that scalariformly pitted elements and the first alternately pitted types are similar in length ($530\ \mu$ and $550\ \mu$, respectively; 15 measurements each). The average diameter for both of these together is $130\ \mu$ (50 measurements). The long, alternately pitted members differ in several ways from the shorter ones found throughout the rest of the wood. The longer elements are narrow and have ends that are slightly constricted toward the rim of the perforation plate. In addition, as already mentioned, the vessel-parenchyma pitting pattern differs because of the vertical length of the axial parenchyma close to the pith.

Mature vessel elements are short with wide lumina and simple, transverse perforation plates and very thin walls (Fig. 13). Some elements have very large tails. Intervascular pitting is alternate, and the pits are crowded so that the chambers may appear slightly polygonal in face view (Fig. 19). Pit apertures are narrowly elliptical to slit-like and are oriented at a slightly oblique angle to the vessel axis. Pitting between vessel elements and axial parenchyma is half-bordered and unilaterally compound (Fig. 14). The border is on the vessel side, and up to eight vessel pits may be opposite a single parenchyma pit field. Often, however, there are several very fine, thickened bars extending across the parenchyma pit field, as well as similar bars in the membrane of the vessel element pit. The pit apertures are extremely irregular in shape and may be elliptical, reniform, or lenticular, with narrow, tapered ends (cf. *Tetrameles*, Fig. 26). When a single vessel pit is opposite a single pit field, the width of the pit field in any direction is usually slightly less than that of the pit membrane of the vessel pit. Occasionally pits to axial parenchyma cells are very small, round, and widely spaced (Fig. 13); this type of pitting can be found on radial and tangential walls but is apparently more common on the latter. Vessels are rarely in direct contact with procumbent ray cells, but in such instances the vessel member pits are similar to the intervacular pits, i.e., the apertures are narrow and the chambers are crowded together. These pits are arranged in conspicuous radial rows, however (Fig. 15). Transitions exist from this kind of pitting to that described for vessel walls in contact with axial parenchyma, just as there are transitions from axial parenchyma to procumbent ray cells. Both types can be found opposite a single parenchyma cell. Tyloses are present in varying numbers in heartwood and sapwood, but they are no more common in the former than in the latter. They are, however, very common (in 12 to 20 percent of the vessels) within a few millimeters of the pith. Pits on tylosis walls are simple and very small.

Figures in the following discussion represent the average of 50 measurements. There is hardly any change in vessel element length and width along a 45 cm radius from near the pith to the cambium. Along this radius element width varies from 220 μ to 330 μ , with a subtle increase radially; and vessel element length (including tails) fluctuates from 430 μ to 520 μ , with no radial correlation. Vessels may be solitary or in pairs. Near the pith up to half of them are in pairs, but along the rest of the diameter frequency varies from 10 to 25 percent. These data are summarized in figures 7 and 9. In transection vessel members are elliptical, with the long axis radially directed (Fig. 17). The vertical course of vessels is usually straight (Fig. 18), but it may be slightly sinuous.

Axial parenchyma is paratracheal vasicentric and forms a sheath two or more cells thick (Fig. 17). The cells adjacent to the vessel element, forming the inner strands, are very flat in transections and are square or broadly rectangular in face view (Figs. 14, 16). The strand ends are truncated. These cells may be divided by vertical or oblique walls as well as by the transverse walls formed in the original cambial derivatives. The number of cells in the inner strands varies from four to 16 but is generally around six; and in the outer strands, from two to four. Length of the strands varies from 500 μ to 600 μ . Although the inner strands have the greater numbers of cells, they are shorter than the outer strands and are the same length as the vessel elements. This is true regardless of the distance from the pith. Cells of the outer strands obviously intergrade with the libriform fibers.

Libriform fiber length increases from 800 μ near the pith to 1300 μ at five centimeters and then to 1700 μ at the outer end of the radius (Fig. 7). Fiber diameter increases from 35 μ near the pith to 50 μ at five centimeters and then decreases regularly to 30 μ at the end of the radius (Fig. 8). Morphologically the fibers can be divided into three zones: the two long, tapering ends and the central "body" having a nearly uniform lumen width throughout and comprising one half to one third of the total length. Pits are confined to the radial walls. The narrowly elliptical to very narrow, slitlike apertures of the simple pits are vertically oriented, and the very thin walls tend to fracture along the pit apertures in macerations. Gelatinous fibers are present in diffuse to concentrated, tangentially arranged groups (Fig. 17). Septae are infrequent in both types of libriform fibers and even in the wood of seedlings. Fibers adjacent to rays have broader lumina than normal, and those differentiating from fusiform initials that have "intruded" within a ray or between two rays are especially broad and are often rectangular in transection.

In the wood seen in this study, no apotracheal diffuse parenchyma is present, although it has been reported in some cases (Burgess 1966). The last source also mentions that the wood may be distinctly ring porous, but no cases of ring porosity were seen here.

Rays may be uniseriate or multiseriate (Fig. 18). Multiseriate rays are heterocellular (Fig. 20). Near the pith only 11 percent of the rays in this sample are uniseriate, and along the remainder of the radius they comprise from two to 15 percent of the total (Fig. 9). Neither abundance nor height of the uniseriate rays shows any distinct correlation with distance from the pith, but there are definite peaks in the

abundance that may correspond to ontogenetic changes in the cambium. More work is necessary for a reliable demonstration of these changes. Multiseriate rays vary from 1400 μ high close to the pith to 1200 μ at the periphery of the bole, and the total range of variation is from 900 μ to 1400 μ . Again there is no correlation of this with position on the radius (Fig. 7). Width of the multiseriate rays, however, increases smoothly from 30 μ at the center to 100 μ at the periphery (Fig. 8).

Uniseriate rays are composed of erect cells only, and near the pith, of course, multiseriate rays are also composed of erect and square cells only. A few millimeters from the pith erect cells are found only at the margins of multiseriate rays, and they vary from narrow and upright to rather broad in radial sections. The maximum height of erect cells observed is about 100 μ . The average for all those measured (150) is 72 μ . Rays initials reaching the maximum apparently divide transversely and two rows of square or even slightly procumbent cells thus result. The several perfect radial sections seen show this change clearly. Changes in erect cells on one margin tend to parallel changes in those on the other margin. Whether the submarginal cells of the two-celled wing change ontogenetically to procumbent cells or to erect cells could not be determined. Height of the marginal cells after the division is from 40 to 50 μ . The rays may have very long wings of erect cells, and up to three multiseriate rays may be connected by uniseriate wings. The total height then often exceeds 3 mm. Wings and rays connected by wings are much more abundant in the inner part of the wood, e.g., wings were present on 25 percent of the rays near the pith in this sample, but none was seen in sections from the periphery of the bole. In other words, ray structure becomes simpler in a radial direction from the pith toward the cambium.

Phloem.—Sieve tube elements of *Octomeles* are arranged singly or in groups much like those of *Tetrameles* (see Fig. 28). They have simple to compound sieve plates and thick, nacreous walls (Fig. 21). Simple sieve plates are always transverse, but not all transverse plates are simple; compound ones are generally oblique, with two to ten sieve areas. The four to twenty-one companion cells are very narrow and deeply staining with fast green-safranin. In transections they are usually triangular and are easily distinguishable from the ordinary phloem parenchyma cells, which are slightly smaller in transectional area than the sieve tube elements and are highly vacuolate. Slime plug material in sieve tube elements is present on sieve areas opposite the lateral primary pit fields of the companion cells but not opposite those of the parenchyma cells. These lateral pit fields are elliptical to irregularly ovate, often with thin bars across the field, and thus they have a scalariform appearance. Pits between sieve tube elements and phloem ray cells are similar. Neither phloem parenchyma nor companion cells have nacreous walls, and both remain in chains in macerations. Cells of the phloem parenchyma strands may divide transversely, longitudinally, or obliquely.

Non-functional sieve tube elements are occluded by tylosoids (Fig. 22, on the right). These arise as expansions of the protoplast of a companion cell into the lumen of a sieve tube element, with a corresponding displacement of the nacreous wall of the latter. Frequently several arise from adjacent companion cells, and

where they meet in the lumen, the cell faces are flat; otherwise, they are spheroidal to elongate. Soon after initial development, most of them acquire thick, lignified walls, as do the corresponding companion cells. Companion cells that do not give rise to tylosoids are still recognizable and apparently do not enlarge. Tylosoids may contain anisotropic crystals and spherites (see Metcalfe and Chalk 1950, p. 700, for a short account of this latter type of inclusion). Pits on and between the tylosoids are simple. Ultimately the entire lumen of a sieve tube element may be occluded by these structures or only a part of it, the rest being crushed by general expansion of the ground tissue.

Secondary phloem fibers and strands of brachysclereids occur in bundles that are tangentially elongate between the phloem rays and are rectangular in transection. In young stems the bundles are frequently radially directed as seen in transection because the rays are so much closer together. This sclerenchyma develops directly from cambial derivatives, and not through sclerification of non-functional sieve tube elements. The phloem fibers are very narrow and elongate, septate, and frequently mucilaginous. Their lumina are almost completely occluded, either by the mucilaginous walls or by lignified walls. Sclerenchyma in the bundles is frequently transitional between simple brachysclereids and elongate fibers; i.e., brachysclereids may have very narrow, elongate tails attached to a short, cylindrical body. These latter are transitional to short fibers that do not show a morphological zonation and have simple, circular pits. The long phloem fibers have slit-like pits that are oriented parallel to the long axis of each cell.

Phloem rays differ slightly from xylem rays. Derivatives of the erect ray initials divide transversely and all the phloem ray cells are thus procumbent, although there is much less radial elongation of these cells than in the xylem rays (Fig. 24).

Dilatation of the rays occurs in the same zone of the phloem tissue in which the tylosoids develop and comes about by both tangential elongation of and divisions in the ray cells (Figs. 22-23). No obvious dilatation meristem is present. Axial phloem parenchyma may divide, but ordinarily it takes little part in the expansion process. Conspicuous intercellular spaces are present in the ray tissue once it begins to expand, and the cells may contain starch, anisotropic crystals, and spherites. Nests of brachysclereids and solitary short-armed sclereids develop in the widening rays, especially adjacent to the strands of secondary phloem fibers. The sclereid nests may extend in either a tangential or a radial direction. The outer layer of procumbent ray cells in contact with the fiber strands is thus obscured (Fig. 23). Sometimes the axial phloem parenchyma strands sclerify, but this is uncommon.

Cambial initials from the cambium of the New Guinea tree used in this study are twice as long as those from the shade-grown seedling. The initials from just above the buttress level average 470 μ long and 24 μ in tangential width. In the seedling stem they average 240 μ and 250 μ long in two different regions of the cambium sampled, and 8 μ wide in a tangential direction. At the level of the buttresses, the sieve tube elements average 500 μ long in both macerated preparations and in tangential sections, and the average longest diameter is 84 μ . Their length corresponds to that of the cambial initials (also cf. vessel element length).

In the seedling the average sieve tube element length is $160\ \mu$, or almost $100\ \mu$ less than that of the cambial initials, and the average longest diameter is $15\ \mu$. This difference can be explained if some of the cambial derivatives divide transversely, or almost so, and the daughter cells undergo only slight elongation. Secondary phloem fibers in the bole from the same level as the sieve tube elements have an average length of $1600\ \mu$ and an average diameter of $40\ \mu$, values corresponding to the dimensions of the libriform fibers in the outer xylem at that level (cf. Fig. 7). Cambial initials in a small branch about 2 cm in diameter average $352\ \mu$ long. The average length of the sieve tube elements in this stem is $307\ \mu$, and the average diameter is $31\ \mu$; phloem fibers average $1360\ \mu$ long and $29\ \mu$ in diameter. In this case the difference between the length of the initials and that of the mature elements possibly results in part from the measurement of slightly elongate derivatives. As mentioned before, the cambium of the small branches is non-storied and is difficult to locate precisely, unlike the storied cambium of the bole. The length of both elements of the phloem here are much shorter than those at the base of the tree. In the seedling two to six companion cells accompany each element, with an average of four. In the phloem at the base of the tree, an average of eight is found, and the most seen was 21.

Tetrameles nudiflora R. Br.

Xylem.—Fusiform cambial initials from the base of the tree from Papua are distinctly storied, as are the ray initials (Fig. 25). Fusiform initials from small branches are not storied. Storying is maintained in all elements of the wood including the rays, but it is not obvious in the vessel elements because they are generally solitary. Initials from the base of the tree have an average length of $520\ \mu$ and an average tangential width of $13\ \mu$.

Primary xylem of *Tetrameles* shows a transitional series in wall thickenings slightly different from that in *Octomeles*. Annular thickenings are present in the earliest formed tracheary elements, but there are also elements with irregularly spiralled bands of very uneven thickness. Regular helical thickenings are single, double, or a combination of each. Complexity of the branching and anastomosis and tightness of the coils increases in a radial direction (Fig. 6). Thin connecting sheets of wall material sometimes unite the gyres of the helices of the morphologically more advanced elements, and vessel elements with scalariform-to-alternate pitting may be found directly adjacent to them (Fig. 4). Transitions in a comparable region in *Octomeles* are usually more abrupt, and vessel elements such as that on the far right in figure 6 are not present in macerations of the xylem of the latter. Often vessel elements with this scalariform-to-alternate pitting have a much greater diameter than the helically thickened elements, and the bars between the pits are very thin. The pits themselves may be hexagonal or polygonal in face view, which is an indication that the elements have been slightly stretched, according to Bierhorst and Zamora (1965). The pitting can be described as scalariform-reticulate in this case. Perforation plates are nearly always simple and vary from transverse to barely oblique, even on opposite ends of the same element (Fig. 5). Transitions

from scalariform-to-alternate (scalariform-reticulate) pitted elements to mature, alternately pitted elements occur over a very short radial distance. The same sort of intermediate vessel members are present here as in comparable regions in *Octomeles* (i.e., comparable in terms of the radial sequence of secondary wall types). The intermediate vessel members are long with ends that are slightly constricted toward the perforation plates, and the pitting is almost identical to that seen in *Octomeles*.

The large, morphologically mature vessel elements are almost indistinguishable from those of *Octomeles* (Fig. 26). Intervascular pits are alternate and crowded closely together; vessel-axial parenchyma pits are unilaterally compound and half-bordered and have ovoid to lenticular or irregularly shaped chambers on the vessel element side. Perforation plates are simple and transverse, and the rim is very narrow. Inner apertures of intervascular pits are sometimes confluent by minute grooves, especially toward the ends of the elements, and very large tails may be present (Fig. 32). Pitting is less common on tangential walls, except when the vessels are in radial pairs; but occasionally normal vessel-parenchyma pit pairs are present on all faces. Vessel element to ray pitting is similar to that between vessels. Short radial files of very small vessel elements are infrequently present among the very large ones throughout the wood (Fig. 29, upper left). Pitting on these is similar to that on the large elements. No such small vessels are present in the wood of *Octomeles*. Lignified tyloses are common in heartwood and sapwood and have very large, simple pits. In transection vessel elements are circular to elliptical with the major axis oriented in a radial direction (Fig. 29), and the course of the vessels is straight to slightly sinuous.

Figures given represent the average of 50 elements measured. Measurements were taken at approximately six centimeter intervals along a 30 cm radius in a section of wood from just above the buttress level of the tree from Papua. Vessel elements of *Tetrameles* are similar in length to those of *Octomeles* but are slightly narrower. Vessel diameter increases hardly at all, as was the case in *Octomeles*, and the change in vessel element length is negligible (Fig. 33). Vessels are solitary or paired, with the pairs of vessels being a little more common than in *Octomeles* but still accounting for only ten to 25 percent of the total (Fig. 11). The number of vessels in a unit area, in this case 0.25 cm^2 , decreases in a radial direction (Fig. 34).

Axial parenchyma is paratracheal, as in *Octomeles*, but the inner and outer strands are both storied and are the same length as the vessel elements (Fig. 30). Strands are mostly two to six cells long, and those nearest the rays are rounded in transection, more like the fibers, rather than tangentially flattened as they are in the rest of the sheath. The thin-walled tissue that appears in transection to be paratracheal, aliform parenchyma is actually composed of fibers, as seen from serial radial sections. Parenchyma is strictly vasicentric in the woods examined here. Axial parenchyma often contains large starch grains.

Libriform fibers increase in length from 910μ near the pith to 1330μ at the end of the radius 30 cm away (Fig. 33). Fluctuations in fiber diameter show no correlation with fiber length (Fig. 35). The fibers are similar in appearance to those of *Octomeles*, but the pits vary from slit-like and inconspicuous to large, with more

noticeable pit membranes (Fig. 32). They show the same tendency to fracture along the pit lines, and the pits are confined to the radial walls. Gelatinous fibers occur in large, tangentially arranged groups, interspersed, of course, with the vessels.

Rays are uniseriate or multiseriate, and the latter are heterocellular (Figs. 30, 31), except near the pith, where the cells are square and erect only. The abundance of uniseriate rays varies from seven to 20 percent and shows no correlation with distance from the pith. There is a peak in abundance in the 18 to 24 cm region (Fig. 10). Multiseriate rays are 1200 μ high near the pith, 620 μ at 6 cm, and 690 μ at 30 cm (Fig. 33). The lowest multiseriate rays are only four cells high. Ray width remains fairly constant along the radius (Fig. 35). Near the pith multiseriate rays are composed almost entirely of erect and square cells, but the ontogenetic change to procumbent cells takes place over a very short distance. Erect sheath cells are rarely present. Uniseriate rays contain square and erect cells only, as seen in radial sections. Frequently a ray consists of two or three multiseriate regions connected by uniseriate wings. These "compound rays" are very numerous toward the pith and decrease in abundance in a radial direction. Wings on rays are also less common in the peripheral wood than near the pith, as was seen in *Octomeles*.

Phloem.—The appearance of the phloem zone with functional sieve-tube elements in *Tetrameles* is similar to that in *Octomeles*. Sieve-tube elements from the base of the tree from Papua (at the same level from which the xylem was taken) are distinctly storied and have thick, nacreous walls (Fig. 27). Sieve plates are transverse or slightly oblique and are either simple or compound. Most oblique sieve plates have two to four sieve areas. Pitting of the phloem elements is similar to that in *Octomeles*, and the arrangement of the elements in transection is the same. Companion cells average 12 in a strand, with a range from 7 to 17. Sometimes two rows of them accompany a single sieve-tube element, and the cells are occasionally divided longitudinally or obliquely. Ordinary phloem parenchyma strands are much larger in transectional area, though not longer than companion cell rows and contain four to eight cells. Sieve-tube elements contain very small starch grains, and the large parenchyma cells contain larger starch grains. Tylosoids are not present, but instead the sieve tubes are obliterated by a general expansion of the phloem parenchyma. Sieve plates, however, are still detectable in a transverse orientation far into the old phloem.

Secondary phloem fibers differentiate directly from cambial derivatives and are arranged in groups between the phloem rays (Fig. 28). The regular rectangular shape seen in transections of *Octomeles* phloem is absent, and small cells of axial and ray parenchyma adjacent to the fiber strands sclerify on their inner and radial walls only, forming what are sometimes referred to as "hippocrepiform" sclereids. These cells frequently contain large, cuboidal crystals, and they give the phloem in longisection a distinctive appearance quite different from that of *Octomeles*, where the adjacent cells are sclerified on all faces. The phloem fibers are usually septate or gelatinous or both.

Phloem rays are non-storied and are similar to those in *Octomeles* (Fig. 27). Expansion of the rays occurs in the zone of non-functional sieve-tube elements.

Ray cells adjacent to the fiber bundles sclerify, but large sclereid nests similar to those in *Octomeles* are infrequent. In general sclerification in the outer phloem region of the bole is not as pronounced as in *Octomeles*.

Cambial initials at the base of the tree have an average length of 520 μ and an average tangential width of 15 μ . Sieve-tube elements at the same level are 480 μ long and 65 μ on the longest diameter. Phloem fibers average 1230 μ long and 43 μ in diameter. Cambial initials from a young branch have an average length of 400 μ and an average tangential width of 12 μ . The average length of sieve-tube elements is 400 μ and the average greatest width, 49 μ ; corresponding sizes for the phloem fibers in the young stem are 940 μ in length and 19 μ in diameter. Once again the phloem fibers are similar in length to the xylem fibers in the part of the wood closest to the phloem cambium.

Datisca glomerata

Xylem.—In the primary xylem of *Datisca*, a series of secondary wall thickening types similar to that in the other two genera is present. Annular and helical thickenings and scalariform pitting occur in vessel elements seen in radial sections and in macerations. The gyres of the helices are more frequently branched and tightly wound in vessel elements that are adjacent to elements with scalariform pitting. The transitional series from helical thickening to scalariform pits to alternate pits on intervascular walls is much less abrupt in *Datisca* than in *Octomeles* and *Tetrameles* because a considerable number of elongate pits and scalariformly pitted areas occur on the earliest alternately pitted vessel members. These areas of scalariform pitting are not necessarily localized at the ends of the elements toward the perforation plates, where the pitting of most vessel elements is frequently modified or distorted, but may occur anywhere on the intervascular face. In stems with a half inch of wood or more, vessel elements near the cambium have mostly alternate intervascular pits, with only a few elongate pits (Fig. 36). Intervascular pits may be widely spaced, but commonly they are very crowded, with chambers that are polygonal in face view and with inner apertures that are ovate to elliptical. The vessels may be arranged in distinct concentric bands or in more or less distinct diagonal bands that intergrade into a diffuse arrangement of vessels in different parts of the same stem.

Axial parenchyma is paratracheal in one or two layers, or around some vessels it is scanty. It is very difficult to recognize in transections because of the thick, lignified walls. The cells are often vertically elongate, and the half-bordered vessel-parenchyma pitting is thus more conspicuously scalariform than in *Octomeles* and *Tetrameles*. These pits are sometimes unilaterally compound. In places where a vessel is close to a ray, the axial parenchyma tends to be flatter and more nearly rectangular in transection, and the vessel-parenchyma pitting is almost identical to that in the two tree genera.

Libriform fibers are short and non-septate and have large, simple pits that are slit-like to elliptical with large, elliptical pit membranes. In some stems gelatinous fibers are absent, but in others they are far more common than non-gelatinous ones.

Rays are uniseriate or multiseriate (Fig. 38). Multiseriate rays are homocellular with erect and square cells in the first 7 mm of wood, but in the outer wood in thick stems there is a tendency for the central cells of the ray to be square and procumbent only. Pits in the tangential walls of procumbent and erect cells are tiny but numerous. Pits on the transverse or radial walls are much larger.

The average length of vessel elements is $200\ \mu$, and the average greatest width, $96\ \mu$. These measurements are taken from the outer xylem of a stem with 7 mm of wood (Davidson 1902). Libriform fibers are $430\ \mu$ long and $14\ \mu$ in diameter. The average height of multiseriate rays is $520\ \mu$, and the average width, $40\ \mu$. In a different stem from the same collection, this time with only 3 mm of wood, the average length of vessel elements is $240\ \mu$, and the average greatest width, $72\ \mu$. Libriform fibers in this stem have an average length of $420\ \mu$ and an average diameter of $23\ \mu$; and the average height of multiseriate rays is $570\ \mu$, and the average width, $45\ \mu$.

Phloem.—Sieve-tube elements have thin, nacreous walls and transverse to slightly oblique sieve plates. Sieve plates are almost invariably simple. Very short-sieve-tube elements have a single companion cell, but the usual number is four. As in *Octomeles* and *Tetrameles*, sieve-tube elements are occasionally solitary in transverse sections, but more often they are in irregular groups or radial rows, and they are generally larger in transverse section than the surrounding phloem parenchyma. The average length of sieve-tube elements is $180\ \mu$, and the average greatest width is $53\ \mu$. Secondary phloem fibers are absent. Dilatation of the rays occurs in the outer phloem where the sieve tubes are nonfunctional, and transverse sections show large "wedges" of dilated ray tissue.

Cambial initials of *Datisca glomerata* are short and show a tendency toward storying (Fig. 39). The average length of the initials is $200\ \mu$, and the average tangential width is $10\ \mu$.

SUMMARY AND CONCLUSIONS

Woods of *Octomeles* and *Tetrameles* are rather similar in appearance and in physical properties. They are light-weight and nondurable and perish rapidly after attacks of fungi and beetles. When dry, they are very weak under most stresses. They have proved useful, therefore, in the manufacture of coffins, match sticks, dugout canoes, tea chests, and carved wooden ware (Burgess 1966; Desch 1941). Anatomically they are very specialized, consisting only of large vessel elements with simple perforation plates, thin-walled libriform fibers, axial parenchyma restricted to two paratracheal layers, and rays. The libriform fibers have very wide lumina and narrow, tapering ends; and they fracture in a nearly vertical direction in macerations, indicating a corresponding alignment or orientation of the cellulose fibrils in the wall. This is possibly a specialization for vertical strength, and a presumed lack of lateral strength resulting from the thin walls of the elements is then compensated by wall hydration. A reasonable assumption is that the wood is somewhat stronger in the living condition than when cut and "green" or dry, and that

the rapid growth of these trees (at least of *Octomeles*) is correlated with this method (wall hydration in the libriform fibers) of attaining strength rather than one involving the production of thick, lignified fiber walls. Zones of gelatinous fibers in the wood are possibly also involved in this function.

The individual elements are similar not only in morphology but also in size. Vessel elements tend to be slightly smaller in radial diameter, however, in *Tetrameles* than in *Octomeles*, and libriform fibers of the former tend to be shorter. Also, vessels in *Tetrameles* are more frequently in radial pairs. The tendency for vessels to be in oblique rows in transections of *Tetrameles* wood mentioned by Lakhanpal and Verma (1965) was not evident in the woods in this study. Trends in the alteration of length and diameter of vessel elements and libriform fibers from the pith toward the exteriors of the boles of the two trees are similar. The most conspicuous difference is the greater amount of storying in *Tetrameles*. All elements of the secondary xylem are storied, including the libriform fibers, a feature that would appear to require a uniform and coordinated increase in the length of the fibers during the increase in girth of the trees. Support for this can be seen in figure 33, which shows a smooth increase compared to that in *Octomeles* (Fig. 7).

Cambial initials of *Datisca* average 200 μ in length and are less than half as long as those at the base of the bole in *Tetrameles* (520 μ) and *Octomeles* (470 μ). Carlquist (1966b) found the same relationship in Compositae: cambial initial length for all caudex perennials studied was half (152 μ) that of the trees (312 μ). Cumbie and Mertz (1963) found in *Sophora* a decreasing conspicuousness of storying in sequence from trees to subshrubs to herbaceous perennials, a situation similar to that in Datisceae. Cambia in *Octomeles* and *Tetrameles* are clearly storied, although some regions in the cambium of *Octomeles* do not show this as well as others; however, the cambium of *Datisca* is not distinctly storied but shows instead a tendency toward that condition, and the fusiform initials are short and similar to one another in length, which is usually the case when obvious storying is present.

The cambium is storied in a wide variety of plants, and the occurrence of this feature surely bears a relationship to habit and the amount of secondary growth that takes place, as pointed out by Cumbie and Merz (1963) and Carlquist (1966b). In *Octomeles* the shortest fusiform cambial initials are in seedlings (250 μ), the largest are in the cambium from the base of mature trees (470 μ), and intermediate sized initials are in twigs (352 μ). In this case the initials elongate considerably over seedling size, but an increasingly evident storied structure in this same sequence results from presumed radial longitudinal divisions. In twigs from a mature tree the vessel elements decrease in size from helical and scalariform (660 μ) to oppositely pitted elements (530 μ to 550 μ), and this apparently reflects a similar change in the fusiform initials.

Scarcity of data on cell lengths in actual storied cambia force one for the most part to extrapolate from vessel element lengths. When compared to published data from both vessel element and cambial initial lengths, these values for Datisceae do not appear to be unusual. The length for *Octomeles* is slightly larger than that given for *Hibiscus tiliaceus* L. (400 μ) and *Picraena excelsa* Lindl. (also 400 μ) (Beijer 1927); and that for *Datisca glomerata* is within the range for plants of

comparable habit (90-200 μ) given by Beijer (1927) and close to that of *Hibiscus lasiocarpus* Cav. (210-212 μ) (Cumbie 1963). Webber (1934) gives the range for vessel element lengths in her material of *Hibiscus tiliaceus* as 59 to 456 μ (mostly 287 μ). Vessel element lengths are given by Hyde (1925) for the following tropical trees with light-weight woods: *Heliocarpus appendiculata* Turcz., 462 μ ; *Apeiba aspera* Aubl., 510 μ ; *Pachira barrigon* Seem., 280 μ ; *Cavanillesia platanifolia* HBK., 675 μ ; *Wercklea insignis* Pitt. & Standl., 300-600 μ ; and *Cordia heterophylla* Poir., 276 μ .

Among the Senecioneae, 62 percent of the species studied by Carlquist (1962) had storied wood structure, and in these vessel element length varied from 463 μ in *Liabum klattii* Rob. & Greenm. and 445 μ in *Gynoxys hallii* Hieron. to 114 μ in *Tetradymia argyraea* Munz & Roos. The species of *Tetradymia*, all occupying a desert habitat, had the shortest vessel elements, and the diminution of elements in xerophytes is well documented in Compositae (Carlquist 1966b). Trees have the longest and caudex perennials, the shortest vessel elements, on the average, among the habit types found in this family. Only six percent of the annuals or biennials employed in this study had storied structure; however, 50 percent of each of the other habit categories, i.e., caudex perennial, shrub or subshrub, tree, and rosette tree or rosette shrub, had it.

From the extensive data of Carlquist (1960, 1962, 1965, 1966a) one can conclude that the degree of expression of storying in the wood is not necessarily related to the length of vessel elements (and hence, cambial initials). In the Astereae (Carlquist 1960) species with short fibers show storying more clearly than species with longer fibers, but storying is not always concerned with the amount of fiber elongation, but instead with the kind of elongation: differentially intrusive or coordinated. This can be seen clearly in *Tetrameles*, in which storying extends through all elements of the wood despite the considerable length of these elements. Presumably there is an upper limit above which the radial longitudinal divisions necessary for the formation and maintenance of a storied cambium are no longer feasible. This limit is obviously above 510 μ .

The trends of change in wood element sizes from the pith outward are interesting to note. Vessel element length remains almost unchanged in both trees throughout the 30 to 45 cm radii examined. In each case vessel element width increases slightly. A similar relationship is present in *Sophora* (Cumbie and Mertz 1963). In contrast fiber length increases 1.6 and 1.8 times the length of the cambial initials close to the pith in *Octomeles* and *Tetrameles*, respectively, and reaches a maximum of 2.7 and 3.8 times initial length at the ends of the radii. According to the table of Chattaway (1936) one might expect an enlargement of 2.0 to 2.3 times the size of the initials for species with initials between 450 μ and 500 μ long. The smaller amount of enlargement and the more uniform increase in length of the fibers in *Tetrameles* compared to *Octomeles* is no doubt at least partly responsible for the persistence of the storied condition in the wood. Fiber diameter in *Octomeles* decreases after a brief increase, but in *Tetrameles* no clear correlation with increasing girth is present. Height of multiseriate rays doubles in *Octomeles* but remains unchanged in *Tetrameles*. Changes in the percentages of uniseriate rays and vessel

pairs present and in uniseriate and multiseriate ray height show subtle peaks and valleys on the graphs that are possibly correlated with environmental changes, especially because the peaks and valleys occur at similar distances from the pith (e.g., at 10 to 15 cm and 25 to 30 cm in *Octomeles*; and at 18 to 24 cm in *Tetrameles*). The number of vessel pairs in $\frac{1}{4}$ cm² as seen in transection decreases greatly. Ray width in mm and fiber diameter show hardly any change except for the slight peaks at 18 to 24 cm in *Tetrameles*, but ray width in *Octomeles* increases dramatically.

The woods of *Octomeles* and *Tetrameles*, although similar in appearance and gross morphology, are thus quantitatively different in numerous respects. The wood of *Datisca* differs both quantitatively and qualitatively from that of the two trees, but this does not necessarily support the recognition of two families, Datisceae and Tetramelaceae, as was done by Airy Shaw (1965). *Datisca* produces much less xylem and the mature wood pattern is much more slowly attained; thus one might expect little obvious correspondence between wood of herbaceous and arborescent members of the same family, as is the case here. The earliest secondary xylem in a stem of *Datisca* is, in fact, unlike that in the bole or even in twigs of *Octomeles* and *Tetrameles*. On the other hand, one might expect that if enough wood were eventually produced in plants with delayed maturation, a pattern resembling that found in trees of the same family would result. The outer wood produced in the largest stems of *Datisca* used in this study definitely has a configuration different from that close to the pith: rays contain a greater abundance of procumbent cells, intervacular pitting is alternate with only a very few transversely elongate pits, axial parenchyma is more conspicuously paratracheal, and the dimorphism in pitting between intervacular walls and vessel element-axial parenchyma walls is more pronounced.

A conspicuous difference in the wood of *Datisca*, however, is the arrangement of vessels in concentric or tangential bands. As far as can be determined, these bands do not correspond to growth rings. The vessel elements within the tangential groupings are all of approximately the same diameter, and the regions between bands are chiefly devoid of vessels; furthermore, definite concentric zones in which fiber diameter increases or decreases are not found either associated with the vessel groupings or in the zones between them. This feature of the xylem represents a major difference that can not be easily explained as simply the result of seasonality of the habitat. *Tetrameles* has been reported as occasionally having ring porous wood, although in the present study ring porousness was seen only in buttresses. An additional study of the buttress wood in *Tetrameles* is in progress.

Thus despite the difference in habits and the amount of wood produced, some correspondence between the woods of *Datisca* and the two Indo-Malesian genera can be noted; this is in addition to the storying or tendency toward it mentioned above.

A specimen of a fossil wood has been described by Lakhanpal and Verma (1965) and is tentatively included in the Datisceae as *Tetrameleoxylon prenudi-flora*. It is from the Deccan Intertrappean beds near Nagpur in Central India and is possibly as old as early Eocene. As described and pictured, its anatomy approaches

very closely that of *Tetrameles*, and the storied structure of the fossil is especially interesting. Storying of all wood elements is very uncommon (S. Carlquist, *personal communication*, 1972). However, several authors (Bailey 1924; Bancroft 1932) have pointed out some of the difficulties in identifying fossil woods and the treacherous convergences of xylem characteristics that may occur (Bailey 1957). In the 1957 paper Bailey stressed the importance of corroborative evidence in making statements about relationships even among living plants.

The anatomical and morphological characteristics of Datisceae indicate a fairly secure phylogenetic relationship with the Flacourtiaceae (Davidson 1973). The features of the xylem allow a modest refinement of this view. The level of specialization of the xylem in *Octomeles* and *Tetrameles* is greater than that in all Flacourtiaceae investigated so far. Values for the libriform fiber/vessel element ratio given by Miller (1975) are predominately below two. The values for Datisceae are: *Octomeles*, 3.95; *Tetrameles*, 2.77; and *Datisca*, 2.15. Vessel elements in Flacourtiaceae are smaller in diameter and in many species tend to be more angular in transection than in Datisceae. Fiber-tracheids are present in many species in addition to libriform fibers, and these elements generally have thick walls and narrow lumina.

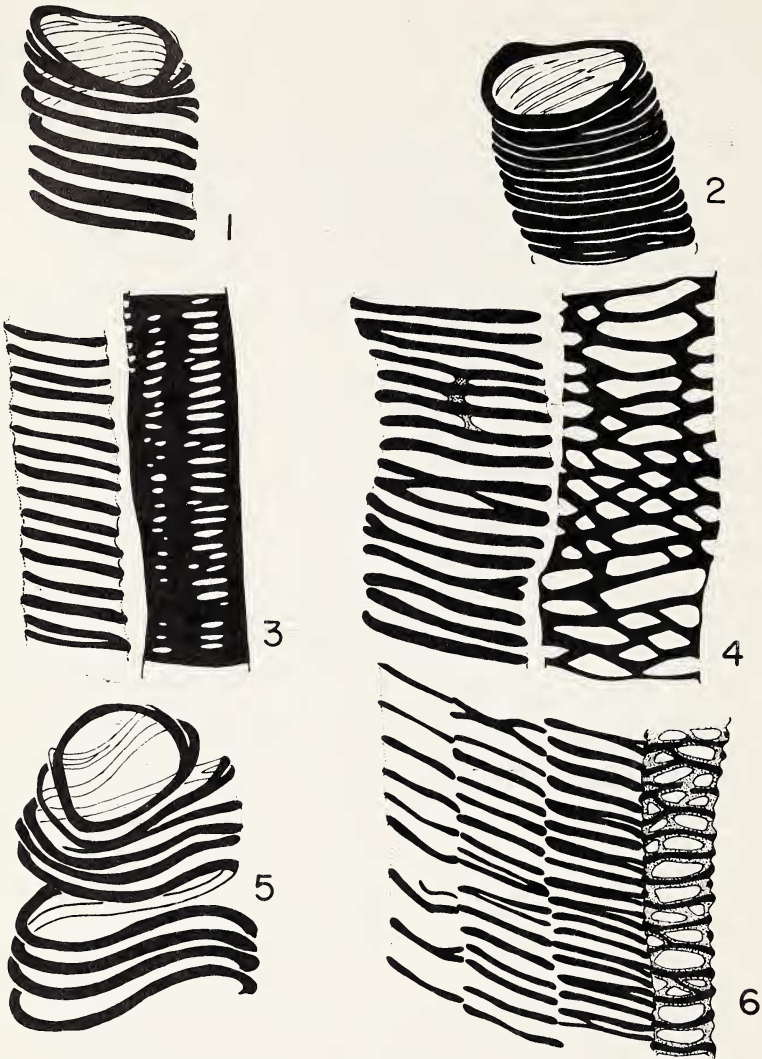
Axial parenchyma is absent in secondary xylem of Flacourtiaceae and is absent or scanty in members of several other families considered to be related within the suborder Cistineae, and for which there is data: Cistaceae (Metcalfe and Chalk 1950), Violaceae (Taylor 1972), and Scyphostegiaceae (Metcalfe 1956). In these three families axial parenchyma, when present, is paratracheal as a few cells about the vessel elements. In Datisceae axial parenchyma is regularly paratracheal in two rows in *Octomeles* and *Tetrameles*; and in *Datisca* it is scanty or absent. Presence of abundant apotracheal axial parenchyma in *Paropsia* and *Soyauxia* indicates the possibility of an early and independent specialization in the xylem (preceding the subsequent and more obvious habit-related specializations) in Thorne's (1968) Caricineae because the tribe Paropsieae (Passifloraceae) is considered a morphologically unspecialized group in transitional between Flacourtiaceae and Passifloraceae (Ayensu and Stern 1964). A similar early specialization in the wood of Datisceae related to rapid growth is a possible consideration independent of the status of the proposed fossil *Tetrameleoxylon*.

Secondary phloem regions of *Octomeles* and *Tetrameles* bear a striking resemblance to one another in the zone of functional sieve tube elements. In each genus the sieve tube elements have nearly the same average length (500 μ) and diameter (ca 70 μ) and have transverse and simple or slightly oblique and compound sieve plates. In addition the lateral walls thicken greatly, apparently as an artifact upon treatment with the fixative, and stain pearly green with fast green. The lumina of the sieve tubes may be almost completely occluded by these walls. Anatomists have referred to them as "nacreous" walls, and their presence appears to be a fairly common feature in the phloem (Esau 1969). Uncommon or infrequently reported, however, is the presence of a large number of companion cells in a single strand accompanying each sieve tube element. In *Octomeles* and *Tetrameles* up to 15 and even 20 may be present opposite a sieve tube element, and they are easily dis-

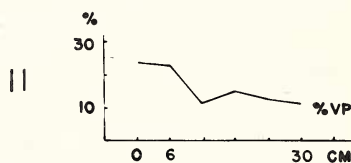
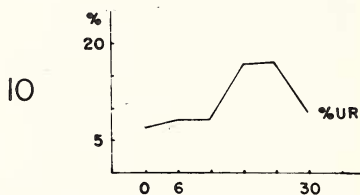
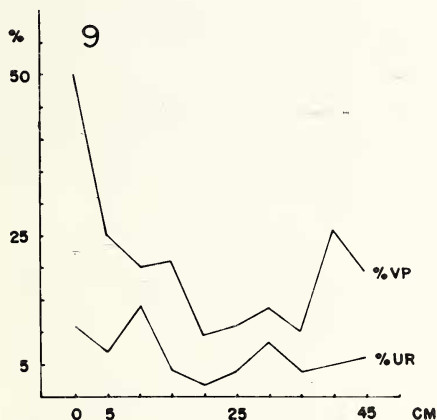
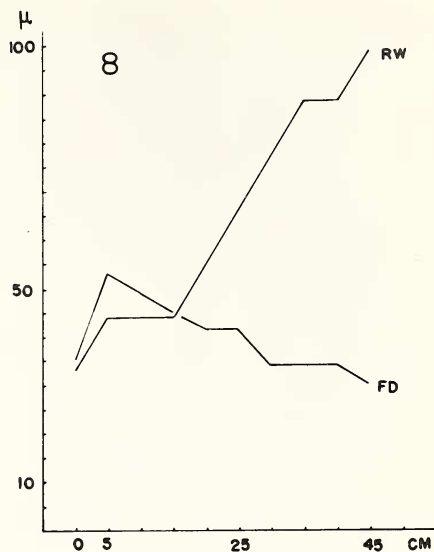
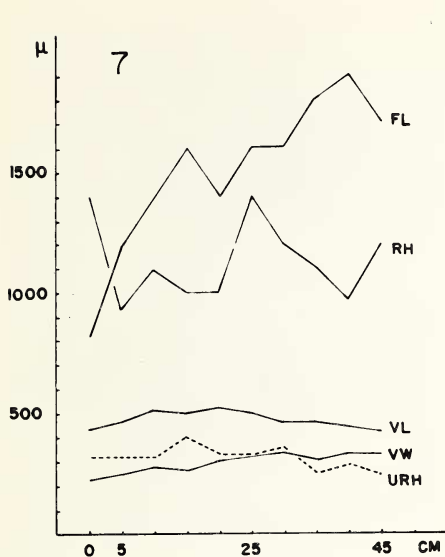
tinguishable from the other phloem elements in tangential, radial, and transverse sections. Secondary phloem fibers differentiate within the part of the phloem containing functional sieve tube elements. After dilation of the phloem rays has begun, the sieve tubes in *Octomeles* are "invaded" by tylosoids that grow out of the companion cells; however, tylosoids are lacking in the phloem of *Tetrameles*, in which the sieve tube elements are obliterated by general expansion of the phloem parenchyma. Moreover, the sclerenchyma that forms around the secondary phloem fibers in this region in *Tetrameles* is composed of "hippocrepiform" sclereids, i.e., they are horseshoe-shaped in transections because the outer cell walls remain unsclerified. Sclereids in a comparable region in *Octomeles* are sclerified on all faces. This is only a minor distinction between the two, but in longisection the outer phloem of each is easily distinguishable because of it.

In *Datisca* secondary phloem fibers are absent, a common feature of herbaceous plants, and the number of companion cells is four to five. Nacreous walls are present, but they are not nearly as thick as in the other two genera; and the sieve plates are almost exclusively simple.

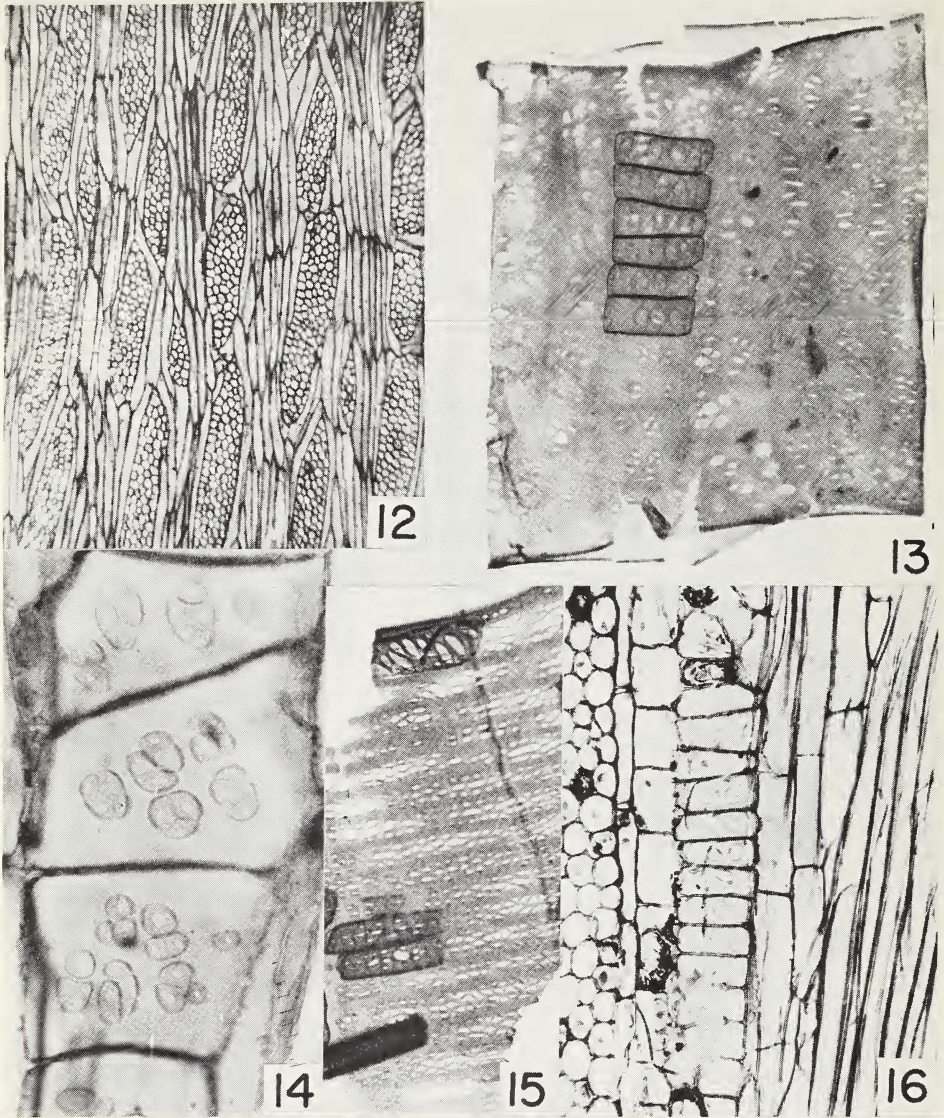
Evidence from anatomy and morphology supports the inclusion of these three genera in a single family. Subfamilial taxonomic ranking is possibly more a matter of personal preference here, but the present writer believes that the differences between Datisceae (*Datisca*) and Tetrameleae (*Tetrameles* and *Octomeles*) do not necessitate subfamily status for the two groups; rather, they are better treated as tribes, as was done by Warburg (1895) and Gilg (1925).



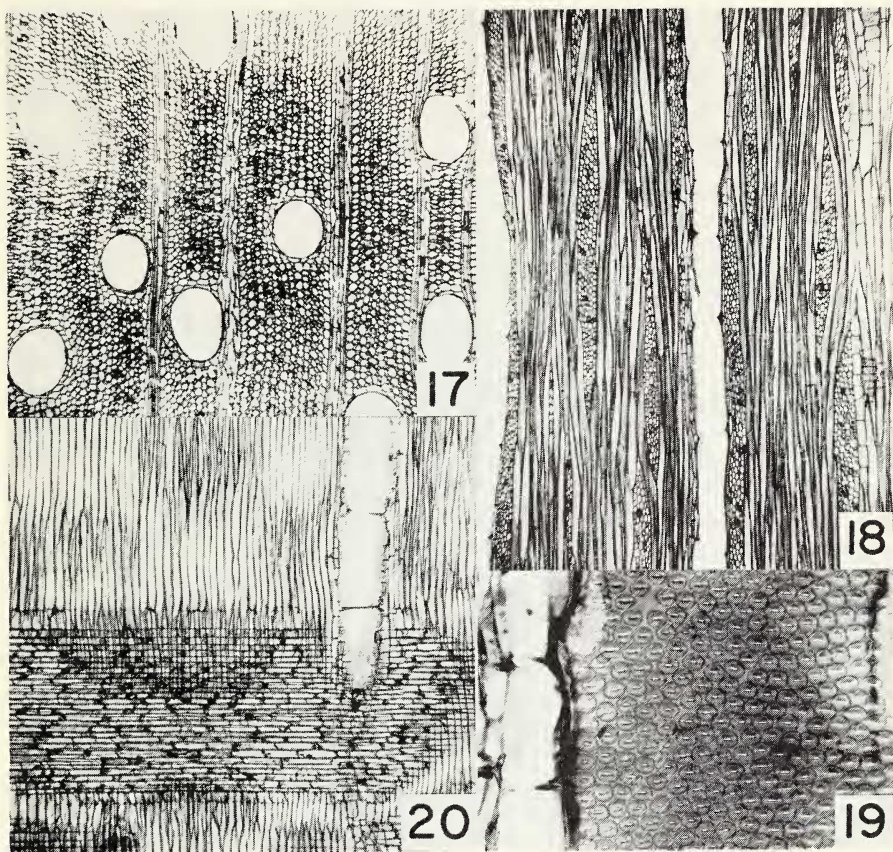
FIGURES 1-6. Primary and early secondary xylem elements, all from macerations. FIGURES 1-3. *Octomeles sumatrana*. Davidson 1127. FIGURES 4-6. *Tetrameles nudiflora*. Davidson 1413a. Drawn with camera lucida. FIGURE 1. Simple perforation plate on a vessel element with helical thickenings. $\times 1200$. FIGURE 2. Vessel element. Very closely spaced gyres with complicated branchings. $\times 600$. FIGURE 3. Two adjacent vessels, one with narrow, scalariform pits. Actual contact between these two elements was obscured. $\times 600$. FIGURE 4. Two adjacent vessel elements. Note three thin connecting walls between the gyres. Parenchyma was present between the two elements. $\times 1200$. FIGURE 5. Simple perforation plate. Note branches in the helix and one thickening band that ends blindly. $\times 1200$. FIGURE 6. Four adjacent elements, each with a progressively more complex thickening pattern. Stippling indicates the wall is more lightly stained than the dark bands. $\times 1200$.



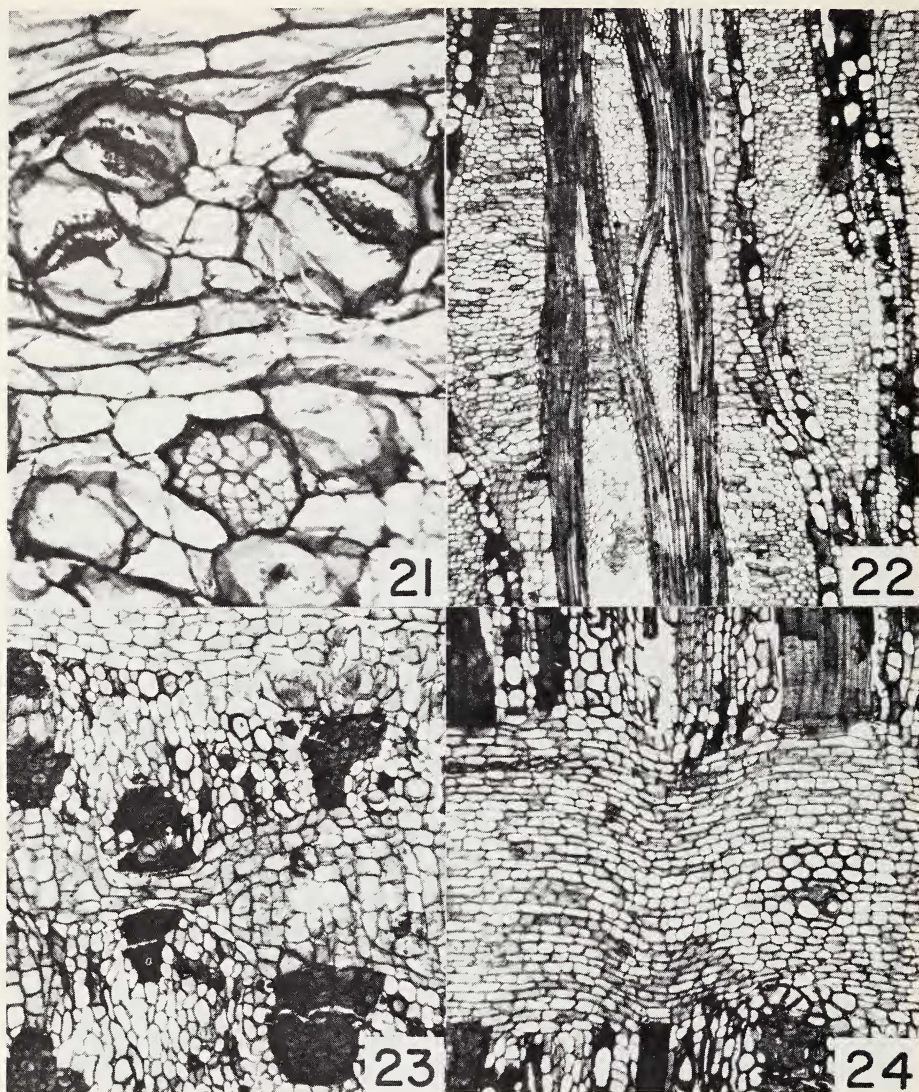
FIGURES 7-11. Graphs showing average lengths and percentages of certain xylem elements (ordinate) in relation to distance from the pith (abscissa) in cm. FD, fiber diameter; FL, fiber length; RH, ray height; RW, ray width; UR, uniseriate rays; URH, uniseriate ray height; VL, vessel element length; VW, longest width of vessel element; VP, vessel elements in pairs. FIGURES 7-9. *Octomeles sumatrana*. Davidson 1482. FIGURES 10-11. *Tetrameles nudiflora*. Davidson 1493. FIGURE 7. Note that fiber length increases but vessel element length changes very little. FIGURE 8. Fiber diameter decreases; width of multiseriate rays increases. FIGURE 9. Note rough correspondence of peaks between the percentages of uniseriate rays and vessel elements in pairs. FIGURE 10. Abundance of uniseriate rays shows a peak. FIGURE 11. Percentage of vessel elements in pairs decreases.



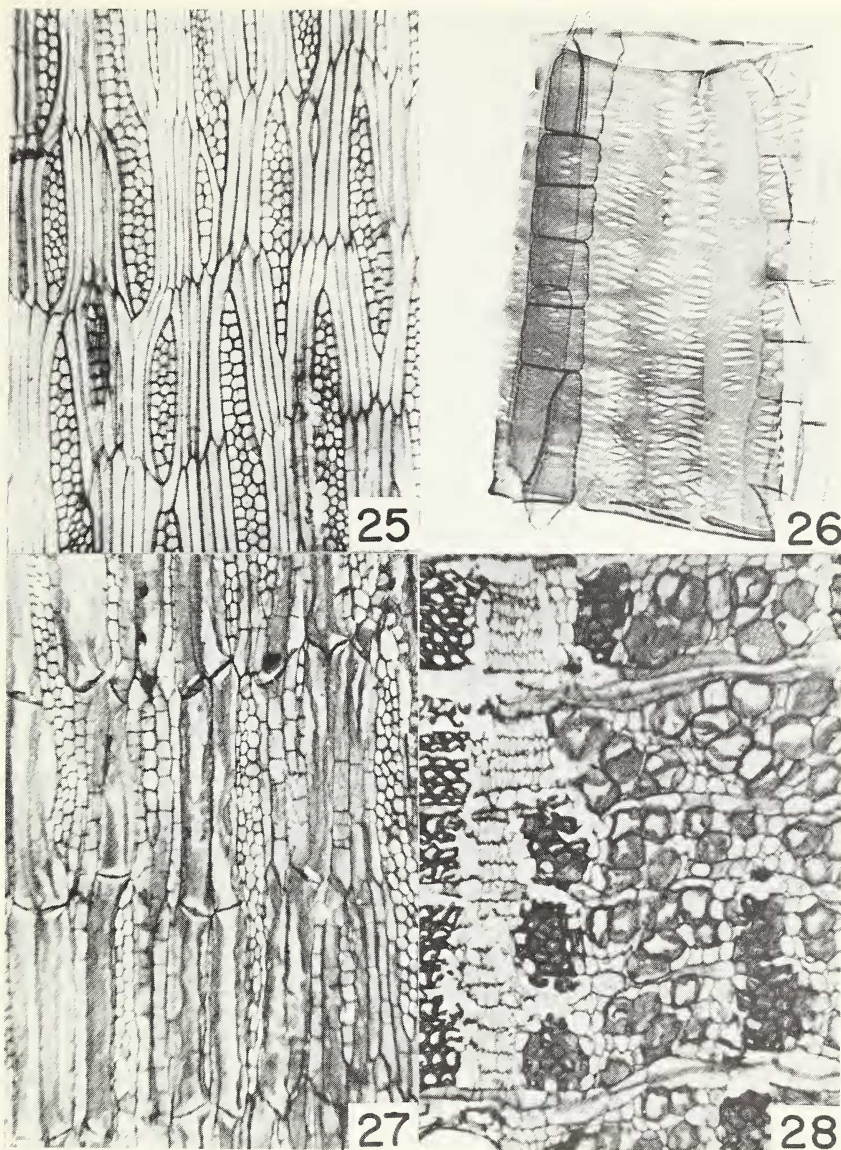
FIGURES 12-16. *Octomeles sumatrana*. Davidson 1482. FIGURES 13-16 from secondary xylem. FIGURE 12. Cambium. Storied condition is most evident on the right. Cambial derivatives are on the far left. $\times 45$. FIGURE 13. Vessel element, flattened by the cover slip. Note unusually small vessel-parenchyma pits. $\times 155$. FIGURE 14. Vessel-to-axial parenchyma pitting. These pits are half-bordered and unilaterally compound. $\times 560$. FIGURE 15. Vessel pits opposite procumbent ray cells. $\times 155$. FIGURE 16. Very long strand of axial parenchyma consisting of sixteen cells. Strand is directly adjacent to the vessel element. $\times 155$.



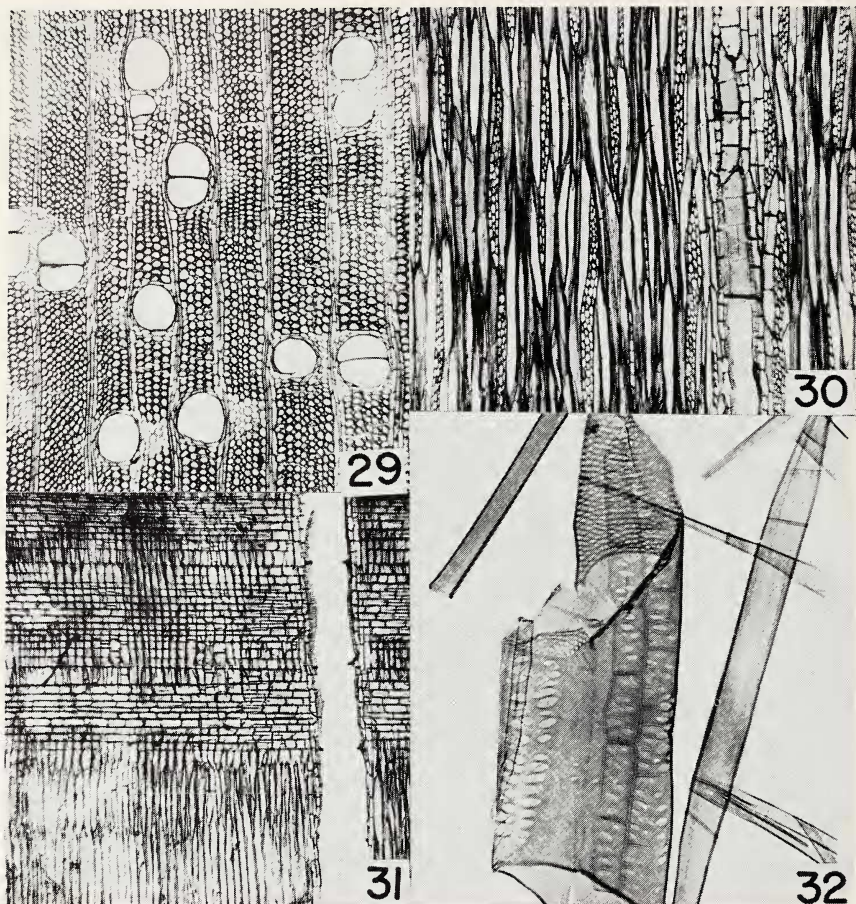
FIGURES 17-20. Secondary xylem of *Octomeles sumatrana*. Davidson 1482. FIGURE 17. Trans-section. Darkened patches are gelatinous fibers. $\times 40$. FIGURE 18. Tangential section. $\times 40$. FIGURE 19. Intervascular pitting. From a tangential section. $\times 360$. FIGURE 20. Radial section. Note erect cells at the top of the ray. $\times 40$.



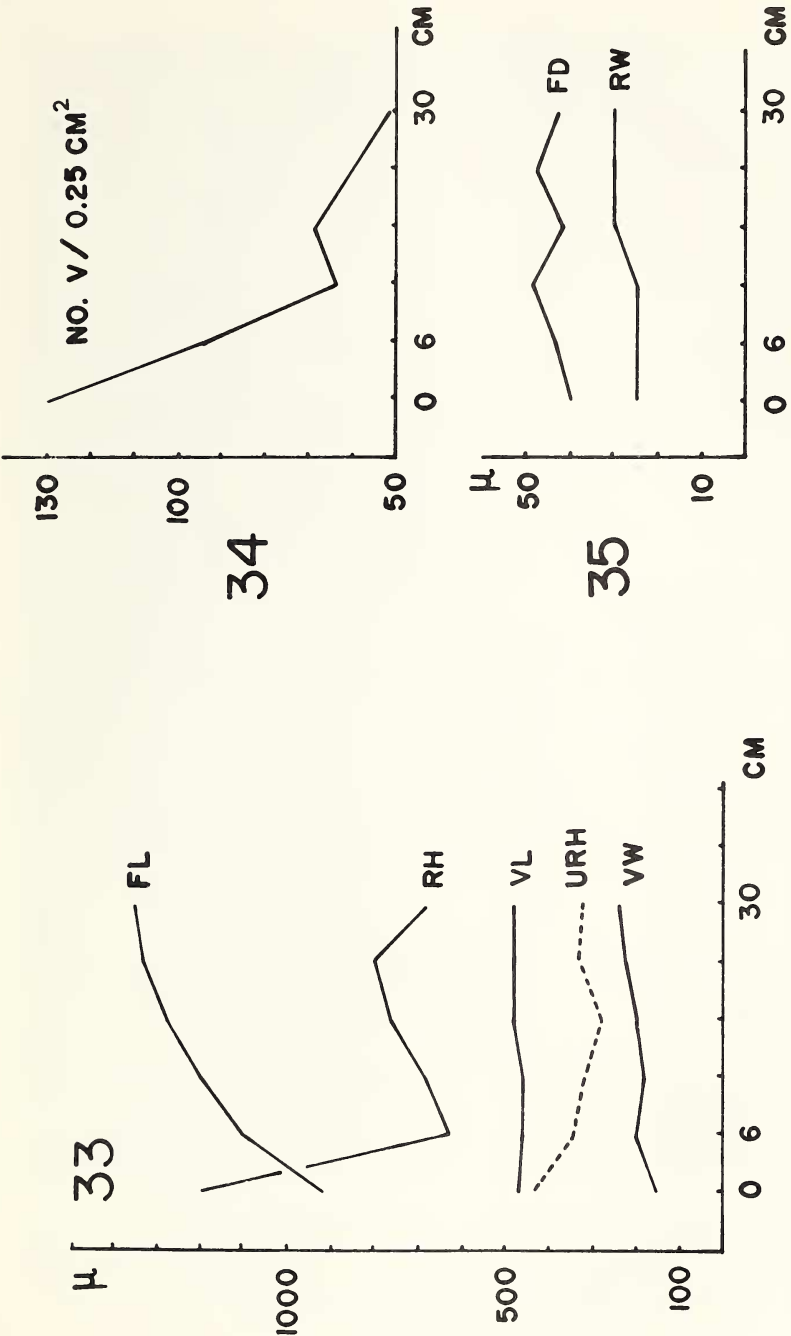
FIGURES 21-24. Phloem of *Octomeles sumatrana*. Davidson 1482. FIGURE 21. Transection of four sieve tubes, three with oblique sieve plates and one with a transverse sieve plate. Note appearance of the nacreous walls. $\times 920$. FIGURE 22. Tangential section through several phloem rays, three of which are undergoing dilation. Secondary phloem fibers are in strands to left of center. Sieve tube elements occluded by tylosoids are to the right. $\times 60$. FIGURE 23. Transverse section showing dilation of a phloem ray and the strands of secondary phloem fibers. $\times 60$. FIGURE 24. Radial section through a phloem ray showing mostly procumbent cells on the left. Cambium is on the left, out of the picture. $\times 60$.



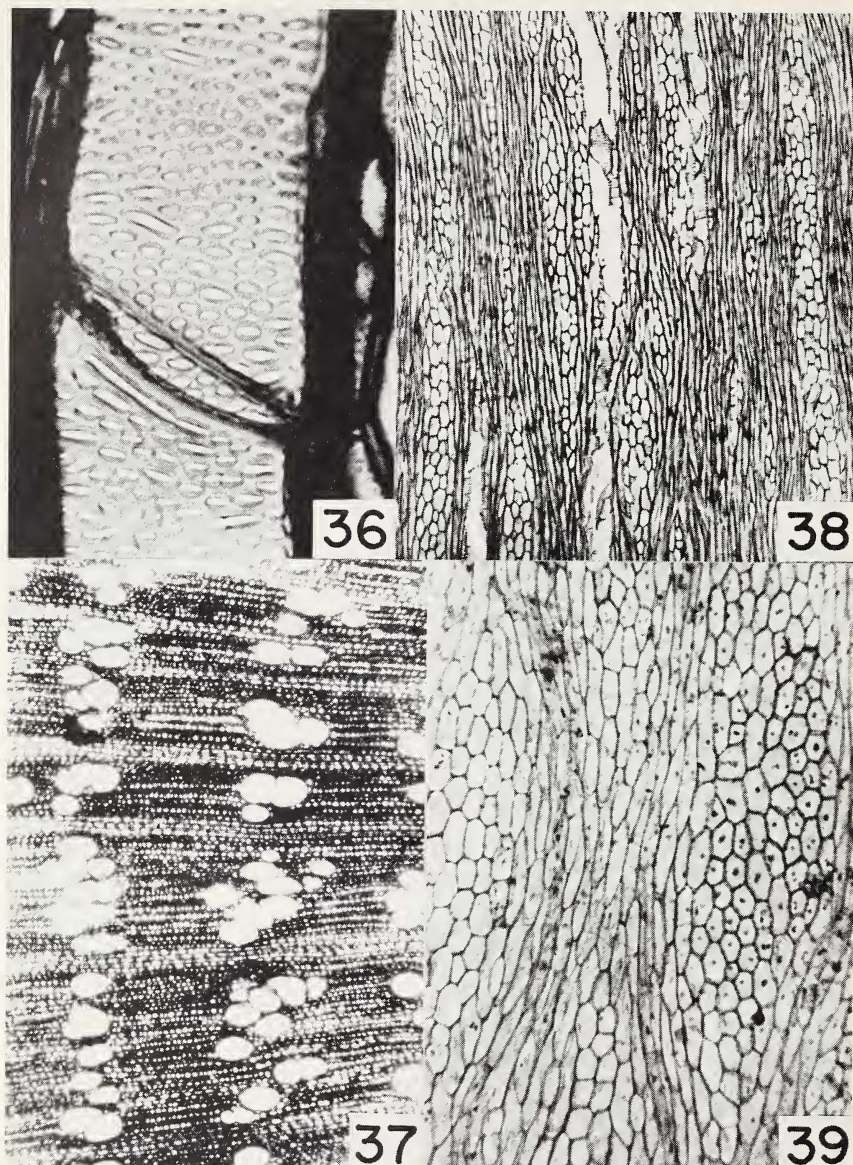
FIGURES 25-28. *Tetrameles nudiflora*. FIGURES 25-26. Davidson 1493. FIGURES 27-28. Davidson 1413. FIGURE 25. Tangential section of cambium region showing storied cambium. Cambial derivatives are on the far left. $\times 70$. FIGURE 26. Vessel element from secondary xylem. Note lenticular pits opposite axial parenchyma cells. $\times 250$. FIGURE 27. Tangential section of the secondary phloem showing storied sieve tube elements. $\times 80$. FIGURE 28. Transverse section of the secondary phloem. Note sieve tube elements with nacreous walls and secondary phloem fibers. Cambium is to the left. $\times 105$.



FIGURES 29-32. Secondary xylem of *Tetrameles nudiflora*. Davidson 1493. FIGURE 29. Transection. $\times 40$. FIGURE 30. Tangential section. Note storied fibers and axial parenchyma. $\times 45$. FIGURE 31. Radial section. $\times 52$. FIGURE 32. Vessel element with a large tail and a few libriform fibers from a maceration. $\times 70$.



FIGURES 33-35. *Terameles nudiflora*. Davidson 1493. Graphs showing average xylem component measurements and number of vessel elements (ordinate) in relation to distance from the pith (abscissa). Symbols are the same as in FIGURES 7-11. FIGURE 33. Note that fiber length increases, vessel element length and diameter hardly change. FIGURE 34. The number of vessel elements in a unit of area decreases greatly. FIGURE 35. Fiber diameter and multiserial ray width change little.



FIGURES 36-39. *Datisca glomerata*. Davidson 1002. FIGURE 36. Intervascular pitting. From a tangential section of secondary xylem. Note simple perforation plate. $\times 340$. FIGURE 37. Transection of secondary xylem showing the ring porous condition in a stem with a centimeter of wood. Pith is toward the right. $\times 55$. FIGURE 38. Tangential section of secondary xylem. $\times 60$. FIGURE 39. Tangential section of stem with one centimeter of wood, showing cambium. Note tendency toward storying of very short fusiform initials. $\times 110$.

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